Harbor Porpoises Utilize Tidally-induced Internal Waves

Little information exists to associate small cetaceans with physiographical phenomena known to affect oceanic prey distribution. We present data which suggest that harbor porpoises, *Phocoena phocoena,* feed in surface slicks generated by tidally-induced internal waves.

Internal waves are evident at the water surface as parallel streaks of flat water ("slicks") surrounded by rippled water in coastal areas and harbors when the wind is light (Ewing 1950; LaFond 1959). Internal waves and the resultant surface slicks are common features in many ocean basins (Ewing 1950; LaFond 1959; Cairns 1967; Hendrickson 1973; Lepley et al. 1977; Shea and Broenkow 1982; Chereskin 1983). The waves often result in areas of increased levels of biological activity due to their tendency to concentrate small organisms (Zelids and Jillett 1982; Kingsford and Choat 1986; Shanks and Wright 1987) and to transport pelagic larval invertebrates and fish (Norris 1966; Shanks 1983, 1988). Fish that feed on plankton concentrated in the internal waves are also aggregated in these areas (Norris 1966; Kingsford and Choat 1986). In addition, cetaceans exhibit affiliations with surface slicks and these animals may feed within the waves as well. Silber (1990) noted that Gulf of California harbor porpoises, *Phocoena sinus,* tended to be sighted more often in slicks caused by internal waves than in surrounding waters. However, there is little quantitative documentation of cetaceans associating with slicks of internal wave origin, nor are there data which suggest that cetaceans feed within the subsurface waves.

In offshore areas, slicks may be caused by different factors, such as windrowing, fronts, and eddies, where waters of differing physical properties converge (Bowman and Esaias 1978). Smith et al. (1986) found that ribbons of increased biomass, represented by intermediate levels of the food web, along fronts or convergent zones were exploited by foraging cetaceans. Researchers in the western North Atlantic reported that sei, *Balaenoptera borealis,* and right whales, *Eubalaena glacialis,* followed offshore slicks as a source of concentrated planktonic prey (Watkins and Schevill 1976, 1979, 1982). Feeding humpback, *Megaptera novaeangliae,* and fin whales, *Balaenoptera physalus,* were also associated with slicks in areas where concentrated schools of fish prey were correlated with dense plankton patches (Watkins and Schevill 1979). Other pelagic cetaceans are known to utilize surface slicks, including pygmy killer whales, *Feresa attenuata* (Pryor et al. 1965), rough-toothed dolphins, *Steno bredanensis,* and false killer whales, *Pseudorca crassidens* (K. S. Norris, Long Marine Lab, 100 Shaffer Drive, Santa Cruz, California 95060, pers. comm.).

During recent field studies on the behavior of harbor porpoises in Monterey Bay, California, we observed that porpoises surfaced most frequently in or near surface slicks. To quantify the association between surface slicks and behavioral activity, a subsequent study was conducted in which harbor porpoise behavior was monitored from a 67.5 meter bluff at Sunset Beach State Park overlooking

Monterey Bay, from 10 September to 1 November 1988, during sea states of Beaufort 2 (no whitecaps, windspeed 7–11 km/hour). The study area consisted of water less than 20 m deep with a sandy substrate. At one-minute intervals, the most recent behavioral state of a focal group (milling or traveling) observed within the previous minute was noted, as was the nature of the water surface (slick or rippled) within which the activity occurred. The first porpoise(s) observed within 1.5 km of the study site was selected as the focal group. If a porpoise group traversed between slick and interslick areas, which occurred rarely, the group was categorized as having surfaced in the water type that it appeared in during its ultimate surfacing. Each surfacing sequence by a porpoise group was treated as an independent event, because we could not be sure whether or not the group under observation had been previously sampled. The minimum observation period for a focal group was set at three minutes for analysis. The width of the slicks was not measured, because the location and dimensions of the slicks and interslick areas were dynamic and constantly shifting.

Traveling was defined as unidirectional movement for at least three surfacings. Milling was defined as nondirectional movement for three consecutive surfacings, generally consisting of criss-crossing or circling movement. Although milling behavior may represent a wide variety of activities in cetaceans and the exact function of milling could not be established in our work, foraging activity in harbor porpoises apparently occurs during milling (Goetz 1983; Watson and Gaskin 1983; Sekiguchi 1987). We saw fish jumping at the water surface near milling harbor porpoises on three occasions, which corroborates, but does not confirm a connection between milling and feeding.

A total of 532 behavioral and associated water surface states was collected on 96 porpoise groups during a total of 19.4 hours on 15 days. Harbor porpoises were generally common within 3 km of shore, but we focused our attention on those animals closest to shore ($<$1.5 km from the observation site), because they were easiest to observe. We used seven power binoculars to spot porpoises.

While in slicks (N = 222), harbor porpoises spent significantly more time milling (N = 139) than traveling (N = 83) (Chi-square = 13.6, df = 1, $P < 0.001$). No significant difference was found between the amount of time spent milling (N = 142) or traveling (N = 168) within rippled (non-slick) water (N = 310) (Chi-square = 2.02, $P > 0.10$). When the two habitats (slick versus non-slick) were compared, a significantly greater tendency for milling while in slicks was found (Chi-square = 24.2, df = 1, $P < 0.001$).

Most harbor porpoise prey items are relatively small gregarious species (Jones 1981), that may be drawn to internal waves to feed on aggregated larvae or zooplankton. In an analysis of harbor porpoise stomach contents from Monterey Bay, Sekiguchi (1987) reported that market squid (*Loligo opalescens*), the northern anchovy (*Engraulis mordax*), the spotted cusk eel (*Chilara taylori*), rockfishes (*Sebastes* spp.), the plainfin midshipman (*Porichthys notatus*), the jack mackerel (*Trachurus symmetricus*), and the shiner surfperch (*Cymatogaster aggregata*) were the numerically dominant prey. Jones (1981) reported that two-thirds of all fish found in stomachs of harbor porpoises from north-central California live in open ocean or are inshore schooling species. The Pacific hake (*Merluccius productus*), the Pacific tomcod (*Microgadus proximus*), rockfishes, and northern anchovies accounted for 97% of all otoliths in harbor porpoise stomachs sampled. Inver-

tebrates, mostly *Loligo opalescens,* were found in 40% of all stomachs examined by Jones (1981).

The tendency for harbor porpoises to affiliate with slicks and to mill while in slicks, suggests that porpoises may be feeding on higher localized prey densities as a result of concentrating properties of internal waves. It is likely that the porpoises were feeding on fish, squid, or other organisms attracted to zooplankton assemblages in the slicks.

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